

MOVEMENT AND MIGRATION PATTERNS IN *PIERIS RAPAE* (PIERIDAE)

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ABSTRACT. Non-migratory movement of the small white butterfly, *Pieris rapae* (L.), was studied in Australia to augment a set of rules developed in the 1970-1980s. Males, like females maintained a preferred direction. *Pieris rapae* was attracted to low vegetation (not necessarily host plants) at distances of 20 m or more. Although daily movement is highly directional, direction reversals occurred at vegetation boundaries. These, and other previously published characteristics of movement, account for many of the patterns of non-migratory movement of *P. rapae*. Migratory movement of *P. rapae* and *P. brassicae* (L.) was studied in the Pyrenees to determine if migration requires additional characteristics. The north-south migration in the central Pyrenees did not extend to adjacent plains. At the northern end of the migration a portion of the *P. rapae* population overwintered while the remainder migrated south. Autumn migrants, moving south, were new individuals of normal size (24.0 ± 0.20 mm wing length) while spring migrants, moving north, varied in age and were large (26.2 ± 0.14 mm wing length). More male than female *P. rapae* were observed in both north and southbound migrations. Migrating *P. rapae* and *P. brassicae* flew straight tracks 1-4 m above the ground at about 8 km/h. Migrants showed no special physiological adaptation for flight at low temperatures when compared with non-migratory individuals. Both migratory and non-migratory *P. rapae* displayed a circadian rhythm that cut off activity at about 1500 hrs even though conditions were suitable for flight. Spring migrants flew in all directions from W through N to E, average direction was away from the sun - but not directly away - and the hourly rate of change was less than the 15° celestial rotation. Non-migratory populations appear to be pre-adapted for migration, requiring only an exaggerated degree of bias in individual directions.

Additional key words: attraction, flight, orientation, *Pieris brassicae*

In 1970, the small white butterfly, *Pieris rapae* (L.) (Pieridae), was selected as a suitable organism for a study of insect movement (Gilbert et al. 1976). The object of the study was to assemble a set of 'rules' which describe patterns of movement, not in one particular environment, but in any environment which the insect normally encounters. A coherent account of several features of the non-migratory movement of *P. rapae* was developed (Jones et al. 1980). The present paper attempts to complete the work by studying several aspects not previously considered, including migratory movement.

NON-MIGRATORY MOVEMENT

The movement of *P. rapae* females during egg laying is an asymmetric two-dimensional random walk (Moran 1968) with two main characteristics (Jones et al. 1980, Root & Kareiva 1984): females are attracted to host plants at distances of about 1 m; and each female maintains a preferred direction of travel during her daily period of egg-laying - but different directions on different days. On some days, preferred directions show a bias, so that more individuals choose one direction than another (Jones et al. 1980). Here, we examine directionality of male movement, and attraction to host and non-host plants at distances greater than 1 m. These studies were carried out in Australia where *P. rapae* shows greater directionality

and less attraction to host plants than in Canada or Britain (Jones 1977, 1987).

Male directionality. In February 1991, at Cockatoo Hill, Bruny Island, Tasmania, an isolated 34 ha paddock of rape (*Brassica napus* L., Brassicaceae) was divided into 40 x 40 m squares (Fig. 1). The paddock was surrounded by eucalypt bush, *Eucalyptus* spp. (Myrtaceae) which butterflies rarely enter (cf. Cromartie 1975). Three squares marked B, C, and D were used as catching sites. The butterfly density was about 60 adult males per square in late January, increasing to 150 on 9 February - about one male (+ one female) per 10 m². After a wet spring, there was a profusion of dandelions, (*Taraxacum* sp., Asteraceae), thistles (*Cirsium* sp., Asteraceae) and wild mustard (*Brassica* sp.) in flower. Butterflies were caught, marked with a felt pen and released in each of seven or more successive half-hour periods (recorded separately) per day, during 14 days from 20 January to 10 February. On other days, weather precluded flight. A different mark was used each day, but individuals were not distinguished. On each day, the mark-recapture procedure was conducted at one site only. A total of 1797 marked males were released, with 49% recaptures including multiples, on the same day, and 16% recaptures one or more days after marking, mostly at the same site.

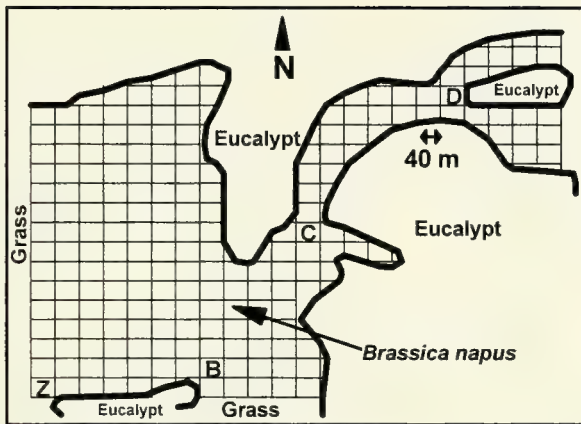


FIG. 1. Map of a paddock of rape, *Brassica napus*, with superimposed grid, February 1991, at Cockatoo Hill, Bruny Island, Tasmania; B, C, and D were mark-release-recapture sites (Table 1); Z was the observation site for *Pieris rapae* crossing marked lines (Fig. 3).

Same-day recaptures permitted maximum-likelihood estimation of N , the number of males present on the square, and q , the retention rate per half-hour within the capture square. The daily average values of q decreased as temperature increased (Fig. 2a), reflecting increased flight activity (Fig. 2b) and emigration. The effect of temperature on male activity is similar to that observed for females (Jones et al. 1980).

Monte Carlo simulations were used to examine directionality of male movements over the grid in Figure 1. Estimated values of q were incorporated into the simulations to account for the effects of temperature. Analyses assumed various degrees of directionality (i.e. of correlation between successive moves). The paddock was represented by numbering the squares and maintaining a list of the four squares adjacent to each square; barriers were represented by listing the same adjacent square twice for squares at the edge - thereby simulating reflection. The program predicted expected numbers of recaptures at different sites one day later. In the field, the highest number of recaptures on the following day arose for movements between sites C and D rather than sites B and C (Table 1, $\chi^2 = 5.6$, d.f. = 1, $p < 0.05$), reflecting the narrow channel between C and D (Fig. 1; Haddad 2000, Sutcliffe & Thomas 1996). A purely random walk, with no directionality, predicted no recaptures at all at different sites over a flight period of 1 day (cf. Fig 4, Jones et al. 1980). Therefore, the values in Table 1 are impossible unless the males maintained some directionality through the day. Simulation results best fit the observed data when the probability of movement from one grid square to the next in the same direction was 0.4. This degree of daily directionality is less than

TABLE 1. Following-day recaptures of marked male *Pieris rapae*, Bruny Island, January-February 1991 (cf. Fig. 1).

Release site	Recapture site	No. released	No. recaptured
B	C	67	2
C	B	102	1
B	C	139	1
C	D	102	2
D	C	120	3
D	C	167	9

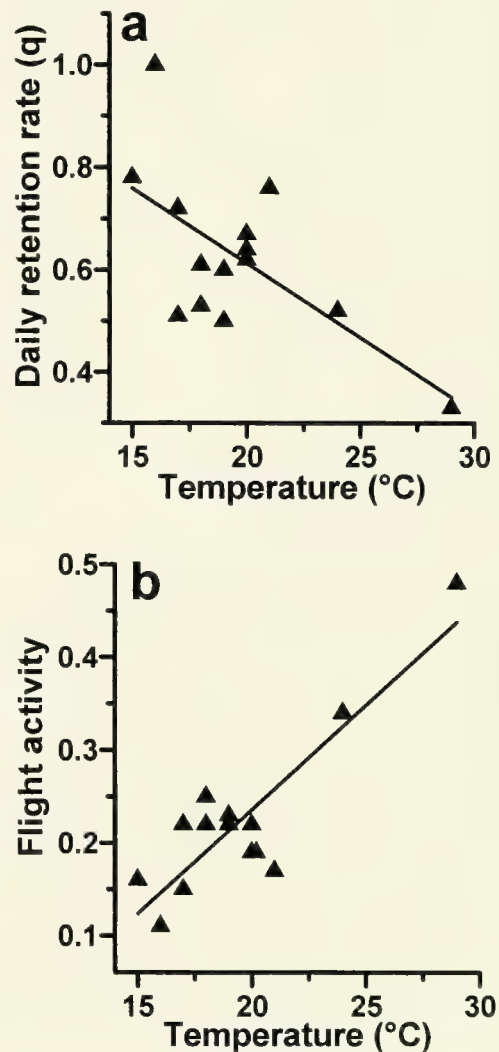


FIG. 2. Daily average retention rate (a), and flight activity (b), of male *Pieris rapae* per half-hour in a 40 x 40 m square within a paddock of rape, *Brassica napus*, at Cockatoo Hill, Bruny Island, Tasmania versus daily maximum temperature recorded at Hobart, Tasmania, February 1991. Flight activity was calculated as the daily average of number of males caught per half-hour, divided by N , the maximum-likelihood estimate of the number of males present. (a) $y = 28.5 - 14.4x$, $r^2 = 0.42$, $p < 0.05$; (b) $y = 11.8 + 34.2x$, $r^2 = 0.77$, $p < 0.001$.

0.6 determined for egg-laying females at Canberra (Jones 1977), but at high population densities, males are continually distracted by interactions with other individuals.

Long-distance attraction to host and non-host plants. The high population density on the Bruny Island rape paddock is typical of summer densities in *Brassica* fields elsewhere in Australia. But adult densities away from *Brassica* fields are much lower. Attraction to host plants at distances of 1 m cannot explain how *Brassica* plots maintain such high local densities. Many of the butterflies which cross the edge of a field in their chosen daily direction, must return.

The behavior of *P. rapae* was studied at the edge of a cabbage (*Brassica oleracea* var. *capitata*) field near Richmond, Tasmania on 22 February 1996. Adult density was similar to that on Bruny Island. Butterflies were observed which had flown at least 2 m over grass, outwards from the edge of the cabbage field. There were no flowers in the area. Of 87 individuals of both sexes, 59 turned back and returned to the cabbages before reaching a fence 20 m outside the edge. The average distance where they turned was 10.2 ± 5.92 (S.D.) m. The other 28 crossed the fence, where they could not be observed reliably. There was an attraction either back towards the cabbage plants, or back towards the resident butterflies at distances of 20 m or more.

Attraction to host plants at distances greater than 1 m was tested in another way. The theory of diffusion (Crank 1975) predicts that butterfly density should decrease rapidly with distance from the edge of a field of cabbages. On 21 February 1994, *Pieris rapae* were counted crossing two marked lines parallel to the edge of the paddock of rape at Cockatoo Hill, Bruny Island, Tasmania (site Z, Fig. 1), one line 60 m outside and the other 10 m inside the paddock. Observations were made during 15 alternating periods, 40 min at the outer line and 15 min at the inner line, throughout the 7 h of main butterfly activity. Counts of *P. rapae* decreased with distance from the paddock, and increasing temperature had less effect on counts outside than inside the paddock (Fig. 3). Egg laying on isolated plants placed at various distances from a cabbage paddock should therefore also decrease with increasing distance. To test this, 10 groups of four 8 week old potted kale (*Brassica oleracea* var. *acephala*) plants were placed in a line leading away from the cabbage field near Richmond, Tasmania on 23-24 February 1996. The first group was just inside the edge of the cabbage field, and successive groups were spaced 2.5 m apart. After two days, the eggs on each plant were counted. Instead of diminishing, the number of eggs increased with distance from the edge (Fig. 4). This does not

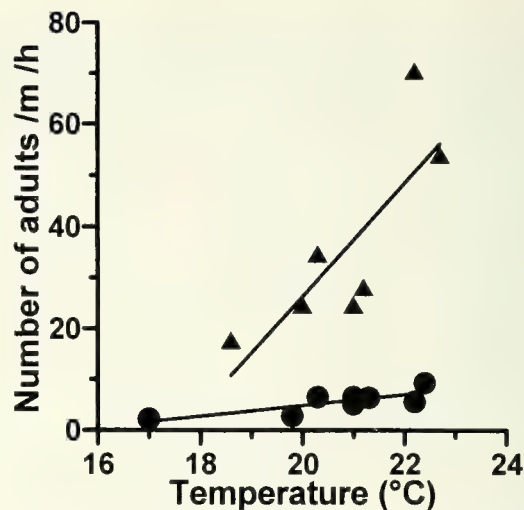


FIG. 3. Number of *Pieris rapae* crossing two marked lines parallel to the edge of a paddock of rape, *Brassica napus*, at Cockatoo Hill, Bruny Island, Tasmania, 21 February 1994 versus temperature. Triangles: line placed 10 m inside the paddock, $y = -195. + 11.1x$, $r^2 = 0.65$, $p < 0.05$, slope S.E. = 3.65. Circles: line placed 60 m outside the paddock, $y = -16.4 + 1.06x$, $r^2 = 0.65$, $p < 0.05$, slope S.E. = 0.322. Slopes are different, $t = 2.7$, $p < 0.05$.

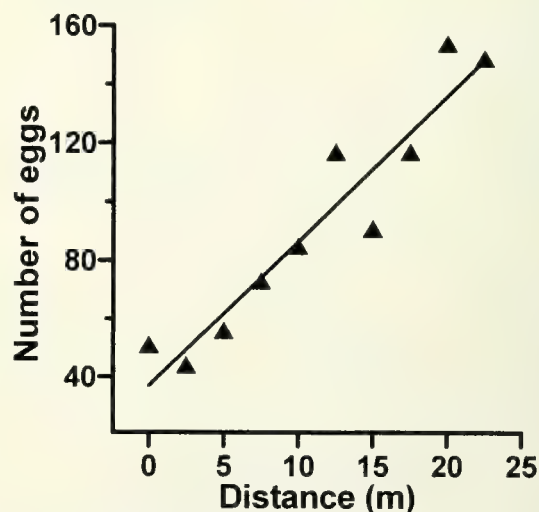


FIG. 4. Number of eggs laid on groups of four kale plants, *Brassica oleracea* var. *acephala* during a 2-day period versus distance from the edge of a field of cabbage, *B. oleracea* var. *capitata* near Richmond, Tasmania, 23-24 February 1996. $y = 37.0 + 4.95x$, $r^2 = 0.90$, $p < 0.001$.

reflect butterfly density, which decreased rapidly with distance. Rather, it reflects attraction of egg-laying females towards the cabbage field at distances of 15 m or more, which counteracted the local attraction to the kale plants. The attraction must have increased closer to the field.

Attraction at distances greater than 1 m is, at least in part, towards vegetation rather than towards other butterflies. In January 1996, a 50-hectare paddock at

Missionary Creek, Bruny Island had recently been ploughed and seeded with rape. There was a 20 m wide stand of unploughed vegetation plus newly-germinated rape, along the creek; but the rest of the paddock was bare and dry. Very few wild butterflies were present. On 16 January, 68 marked adults were released along the creek. On the following day, 71% were recaptured at the same place between 0945-1315 hrs. By 13 February, after heavy rains, the entire paddock was covered in rape plants. Of 84 adults released in similar conditions, only 24% (the same for males and females) were recaptured the next day between 1015-1445 hrs, and catches on the following day confirmed that the butterflies had dispersed over the paddock. When the paddock was bare, they remained with the vegetation along the creek; but when the paddock was well covered with plants, they dispersed.

Two studies suggest that longer-distance attraction is towards scrub vegetation, not just Brassicaceae. First, 200 adults were released on 26 January 1991 in seashore vegetation at Adventure Bay, Bruny Island. Of 14 which subsequently flew out of the vegetation over sand dunes, all promptly returned. There appeared to be no Brassicaceae in the vegetation. Second, between 0915-1215 hrs on 1 and 2 November 1997 in clear sun, 22-27°C, at Atherton, N. Queensland, *P. rapae* adults were observed entering a 20 x 40 m vegetable patch containing no Brassicaceae, and an adjacent 16 x 40 m grass paddock (with 16 m common border). *Pieris rapae* was scarce in the area; sometimes one, never more than two butterflies were seen at a time. Females were caught and males were watched as they flew out of the area. Therefore, every observation represented a new arrival - if not a new individual. In 6 h, 19 *P. rapae* were observed in the grass paddock and 53 in the vegetable patch, significantly different from expected values given patch size and assuming no patch preference ($\chi^2 = 9.5$, d.f. = 1, $p < 0.01$). Of the 19 butterflies observed in the grass paddock, 10 left for surrounding grassland, but 9 entered the vegetable patch, a disproportionately large number ($\chi^2 = 17.0$, d.f. = 1, $p < 0.01$) given that only 16 m of the 112 m grass paddock perimeter was adjacent to the vegetables.

MIGRATORY MOVEMENT

Characteristics of *P. rapae* and *P. brassicae* (L.) movement were examined in the Pyrenees, over which these species migrate annually (Lack & Lack 1951, Williams et al. 1956), to determine what additional characteristics are needed to explain the movement pattern of migratory individuals. Because little is known of this migration we first consider the general features: taxonomy of the migrating species; geographical extent

of the migration; proportion of the population that migrate rather than diapause; age and size of spring vs. autumn migrants; and sex ratio of the migrants. We then consider specifics of freely migrating butterflies: velocity, light and temperature required for flight; circadian rhythm for flight; and directionality.

General features of the migration. Williams et al. (1956) found that the most common migrating species were *P. rapae* and *Colias croceus* (Geoffroy); five other migrating species were abundant and four were rare. There has been some confusion, however, with respect to identification of *P. rapae*. In the Mediterranean, *P. rapae* is easily confused with *P. ergane* (Geyer), *P. manni* (Mayer) or *P. napi* (L.). Whereas British *P. napi* always bear green wing markings, Mediterranean individuals lack this pigmentation if the pupae are exposed to high temperatures in the laboratory or in the field. Breeding experiments at 20°C confirmed that the trans-Pyrenean migratory species is *P. rapae*, not *P. ergane*, *P. manni* or *P. napi*. Most of the following observations and catches were made at a level site at altitude 1630 m in the upper Ariege valley ('A', Fig. 5), where there are no resident populations of these species.

The migration is well documented along the middle length of the Pyrenees (Lack & Lack 1951, Williams et al. 1956). At either end, the situation is less clear. At the Atlantic end, Snow & Ross (1952) reported a migration of dragonflies, but no butterflies, near Hendaye. At the Mediterranean end, Williams et al. (1956) reported a southward migration of butterflies, including *P. rapae* in autumn, but noted "Whites" flying both north and south. Spieth and Kaschuba-Holtgrave (1996) reported an autumn migration of *P. brassicae* WSW at Perpignan (Fig. 5). Our observations at Carcassonne, and Rivesaltes near Perpignan (Table 2), when the autumn trans-Pyrenean migration was in full spate, do not confirm reports of a migration. Furthermore, on 23 September 1992, during the main migration, nine *P. rapae* were caught and marked in the morning at le Racou, Argelès, where Williams et al. (1956) made observations; five were recaptured that afternoon, and two the following day. There was no sign of migration at the eastern end of the Pyrenees. In the middle of the range, the migration of both *P. rapae* and *P. brassicae* appears confined to the Pyrenees. It did not extend to the adjacent plains where there were resident populations which showed no sign of migration (Table 2).

The trans-Pyrenean *P. rapae* and *P. brassicae* have the same temperature thresholds for larval development, 10°C and 9°C respectively (Gilbert & Raworth 1996), as their conspecifics elsewhere (Gilbert 1988, and

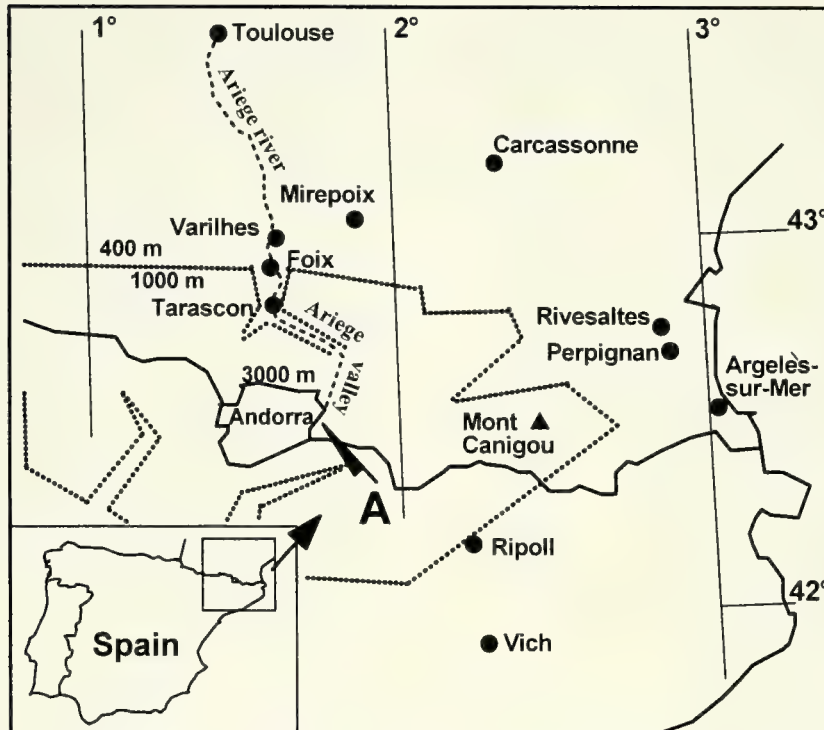


FIG. 5. Map of the Pyrenees and surrounding area; arrow at 'A' marks the sample site in the Ariège river valley at 1630 m altitude; Coll dels Clots, another sample site (Table 3), lies 1.5 km N of 'A' at 2170 m altitude. The fine dotted line marks ~1000 m elevation; 3000 m peaks generally run along the border between Andorra and France.

unpublished data). It follows that slow larval development in winter is possible at the south side of the Pyrenees, but not at the north. Therefore, *P. rapae* and *P. brassicae* which spend the summer on the north side of the Pyrenees can either pass the winter in diapause, or migrate south to produce an active generation through the winter. Migrant *P. rapae* were caught in June 1995 and bred through two generations under field conditions at Cambridge; second-generation eggs hatched 25 August and average pupation date was 20 September. When pupating at the September equinox, 23 of 33 pupae entered diapause and the rest emerged later in autumn - by contrast, all of 45 local Cambridge pupae diapaused. The proportion entering diapause *in situ* in the Pyrenees is unknown, but certainly some; for on 26 April 1996, 26 *P. rapae* (25 ♂; 1 ♀) and 23 *P. brassicae* (13 ♂; 10 ♀) were caught at Tarascon (480 m), long before the northwards migration (Ariège valley site 'A', Table 2) had begun.

The physical characteristics of spring and autumn migrants of *P. rapae* were different. During 4 consecutive years, 114 northbound and 40 southbound individuals of both sexes were caught and measured, and many more were observed in flight or feeding. Those going south in autumn were all new individuals with undamaged white wings and very black markings;

old individuals have frayed, yellow-green wings and pale markings. They were of normal size with wing lengths 24.0 ± 0.20 (S.E.) mm, corresponding to average pupal weight of 150 mg (Jones et al. 1982), and some at least were not ready to lay eggs - determined by placing twelve females in several cages with kale plants. Those going north in spring were of varying ages, but exceptionally large with wing lengths 26.2 ± 0.14 (S.E.) mm, corresponding to average pupal weight of 180 mg, and the females were mated and ready to lay. When bred on kale at 20 and 26°C, the progeny of the large spring-migrant *P. rapae* were the same size as *P. rapae* elsewhere. During the spring migration, *P. rapae* are so large that they are difficult to distinguish from small *P. brassicae*.

Males always predominated in the migration. In samples collected in 4 successive years under clear sun at 16-19°C, totals were: northbound, *P. rapae* 101 ♂: 13 ♀, *P. brassicae* 9 ♂: 7 ♀; southbound, *P. rapae* 27 ♂: 13 ♀, *P. brassicae* 38 ♂: 21 ♀, *C. croceus* 15 ♂: 7 ♀. These ratios, which are significantly different from 50:50 (d.f. = 1, $p < 0.05$) for southbound ($\chi^2 = 4.9$) and northbound ($\chi^2 = 67.9$) *P. rapae* and southbound *P. brassicae* ($\chi^2 = 4.9$), are not artifacts of catching because males, being stronger fliers than females, are harder to catch. In contradiction, Gray et al. (1953) observed *C. croceus* 30

TABLE 2. Observations of the movement of *Pieris rapae* and *P. brassicae*, flying on clear sunny days in the Pyrenees and on adjacent plains to the north and south (Fig. 5).

Location ¹	No.	Movement ²	Conditions
Carcassonne	15 <i>P. brassicae</i>	not migrating, flying NE	1000-1100h, 4 Oct. 1992
Rivesaltes	17	not migrating	29 Sept. 1996
Mirepoix	-	not migrating	p.m., 6 Oct. 1994
Varilhes	7 <i>P. rapae</i>	flying S, 9 flying N	1330-1500h, 27 Sept. 1994, max 21°C
Varilhes	-	not migrating	1100-1200h, 6 Oct. 1994, 17°C
Foix	4	migrating S	1100-1130h, 27 Sept. 1994, max 21°C
Ariege valley (site 'A')	6♂, 5♀ <i>P. brassicae</i> caught; 87♂, 8♀ <i>P. rapae</i> caught; 71 not caught	migrating N-NW:	27-28 Jun. 1996, max 19°C
Ariege valley (site 'A')	222	migrating (Tables 3, 4)	30 Jun.-1 Jul. 1996, max 19°C
Ripoll	-	not migrating	29 Jun. 1996, max 27°C
Vich (Vic)	>24 <i>P. rapae</i>	not migrating	29 Jun. 1996, max 27°C

¹ Varilhes is at the southern edge of the plain, Foix is just in the foothills.

² Butterflies flying straight tracks in a limited set of directions were defined as migrating; those flying non-linear tracks or where preferred directions were all round the compass, not migrating.

♂: 68 ♀, at another location. However, in their study, sex was determined while the butterflies were in flight - a difficult task. Egg-laying females are easily distinguished from prowling males but these behaviors do not apply during migration.

Characteristics of movement of migrating individuals. The main barrier to migration in the Pyrenees is the central chain of mountains 40 km wide which rise to altitudes of about 3000 m. Migrating *P. rapae* and *P. brassicae* (Table 3) flew in straight tracks 1-4 m off the ground, uphill or downhill, stopping to feed when they encountered flowers. Mean velocity, measured in calm conditions by running with the butterflies for 100 m on level ground with a stop watch, was about 8 km/h (n = 10); Williams et al. (1956) estimated flight speed at 8-16 km/h. One day therefore affords ample time to cross the central 40 km. However, the mountains are generally obscured by clouds. Migration continues when it is partly cloudy and some blue sky is visible, but stops when clouds completely cover the sky (Williams et al. 1956, confirmed by observations of migrations from 1994-97).

The butterflies often have to wait several days for the sun.

At sea level, *P. rapae* flies at temperatures exceeding 15°C in sun, and exceeding 20°C under clouds (unpublished observations during 20 years). Between 15 and 20°C, the butterflies warm themselves by basking in the sun. This agrees with the observation that *P. rapae* caught in flight always have thoracic temperatures $\geq 20^\circ\text{C}$ when measured with a thermocouple and electronic thermometer (n = 41, including 16 butterflies in Tasmania and 25 migrants in the Pyrenees, at 20°C and 15°C air temperature, respectively). But at 1630 m altitude, migrating butterflies fly in sun at air temperatures as low as 9°C (Williams et al. 1956, confirmed by observations of migrations from 1994-97). When 15 *P. rapae* of Pyrenean migratory stock were caged at sea level with 15 butterflies from Cambridge, individuals from both sources became active in sun at 15°C, which indicates that there is no physiological adaption to lower temperatures in trans-Pyrenean stocks. Presumably the greater irradiation at altitude enables the butterflies

TABLE 3. Counts of migrating *Pieris rapae* and *P. brassicae* (not distinguished, but mostly *P. rapae*) observed over 30 x 30 m areas, Ariege valley ('A', Fig. 5) at 1630 m, except Coll dels Clots at 2170 m (CdC); with sun times and air temperatures (T). Full sun, still days, 1996.

Sun time (hrs.)	0730- 0830	0830- 0930	0930- 1030	1030- 1130	1130- 1230	1230- 1330	1330- 1430	1430- 1530	1530- 1630
28 June T(°C)	16	16.5	18	18	18.5	19.5	19.5	19	18.5
Migrants	4	5	13	17	21	36	29	11	0
30 June T(°C)		14.5	15.5	16	17	17.5	18	19	
Migrants		11	25	32	31	40	26	12	
1 July T(°C)		14	14.5		20		17.5		
Migrants		5	18	—	11(CdC)	-	22		

to warm up at air temperatures below 15°C. In June and October, temperatures in the Pyrenees at 1630 m exceed 9°C through most of the day in fine weather, so temperature is not a limiting factor.

Pieris rapae has a circadian rhythm. Its timing has been estimated by experiments on females caged at Hobart, Tasmania in clear sun at temperatures remaining above 20°C until 1800 hrs (sun time). Control females were free to lay all day (six gravid females in one cage and seven in another produced 79.8 eggs per female). Another 13 gravid females were deprived of host plants until specified times. After being presented with host plants at 1400 hrs, six of these females laid 63.8 eggs per female; when presented with host plants at 1500 hrs the remaining seven females laid 23.9 eggs per female, and very few eggs were laid after 1600 hrs. Counts of migrating *P. rapae* and *P. brassicae* in the Pyrenees also declined abruptly between 1500-1600 hrs (Table 3), even though conditions were suitable for flight.

Migrant *P. rapae* and *P. brassicae* were observed in the Ariege valley and surrounding hills ('A', Fig. 5) in June and July 1996. The Ariege valley runs SW - NE at the observation point. There was more scrub vegetation in the valley than on the surrounding hills. Migrant directions varied from W through N to E. Those which crossed the valley at right angles flew straight uphill NW, with no obvious tendency to deviate along the valley. The first 2 days of observation established the daily time pattern on the valley floor (Table 3). On the third day, the observer began on the valley floor, then climbed 500 m following the average direction of migration (NNE), and subsequently returned. There appeared to be more migrants in the valley (counts between 0830-1030 hrs and 1330-1430 hrs) than higher up (counts between 1130-1230 hrs), but the difference was not significant ($\chi^2 = 3.2$, d.f. = 1, $p > 0.05$). The average direction vectors of migrating *P. rapae* and *P. brassicae* followed the sun through the day (Table 4),

but the average direction was not directly away from the sun, and the hourly rate of change was less than the 15° celestial rotation.

DISCUSSION

Non-migratory movement. Non-migrating male *P. rapae* exhibit some directionality. This directionality increases the radial distance moved, and may increase their chances of finding new mates, just as female directionality increases the chances of finding new host plants (Jones et al. 1980).

Jones et al. (1980) found that movement of non-migratory *P. rapae* is highly directional each day. Daily direction is, however, influenced by field boundaries because 70% of individuals that left a *Brassica* field in the current study, reversed direction at 20 m or more, and returned. Schtickzelle & Baguette (2003) observed similar direction reversals at boundaries in *Procllossiana eunomia* Esper (Nymphalidae), and found that patch area and landscape fragmentation affected emigration.

The probability of *P. rapae* emigrating from a field was not determined, but the relationship between egg-laying and distance from a field (Fig. 4) suggests that attraction to a field at 25 m is considerably less than at 1, or 10 m. Furthermore, 30% of *P. rapae* observed flying away from a field flew beyond a fence at 20 m. These observations suggest that there may be considerable patch-to-patch movement in *P. rapae*, as has been observed for *Hesperia comma* L. (Hesperiidae) (Hill et al. 1996) and *P. eunomia* (Baguette & Nève 1994). Attraction to low vegetation at distances up to 20 m

TABLE 4. Average directions of migration (S.E. \pm 7.3°), Ariege valley ('A', Fig. 5), 30 June to 1 July 1996 (cf. Table 3). 0° is N, 90° is E. Individual directions varied from W through N to E.

Sun time (hrs)	0830-1030	1030-1230	1230-1330	1330-1530
Direction	21°	24°	52°	54°
n	59	63	40	60

would adapt *P. rapae* to finding host plants in patchy environments where mixes of host and non-host plants occur.

Five characteristics account for many of the patterns of local and long-distance (1-2 km) movement of non migratory *P. rapae*: daily directionality in males and females, sometimes biased (Jones et al. 1980, Root & Kareiva 1984); attraction to host plants at distances of about 1 m (Jones et al. 1980); attraction to flowers (Root & Kareiva 1984); attraction to low vegetation (not necessarily host plants) at distances of 20 m or more; and interactions with other individuals (Hertz 1927).

Migratory movement. The different physical characteristics of spring and autumn *P. rapae* migrants implicate different forces driving the two migrations. The autumn migrants, being of normal size and young, must experience warm summer temperatures as larvae (Gilbert & Raworth 1996), and on emergence immediately fly south. They thereby escape winter and produce the next generation in Spain while a portion of their cohort diapause north of the Pyrenees. The spring migrants, being large and old, must experience winter temperatures around 10°C as larvae (Gilbert & Raworth 1996), and spend some time as adults in Spain before migrating north. In southern France, including Tarascon at the northern edge of the Pyrenees, *P. rapae* emerges from winter diapause during April and May. There is then a period in June when adults and larvae are scarce or non-existent, despite the abundance of young *Brassica* plants. Therefore, the trans-Pyrenean migrant females find an empty niche, while the males must wait for the appearance of second-generation adult females, which at Tarascon begin to emerge around the end of June, very soon after the migration.

The orientation-navigation system for trans-Pyrenean *P. rapae* appears to be different from *Danaus plexippus* L. (Nymphalidae). Migrating *D. plexippus* use various cues, including the physiographic features of the Sierra Madre Oriental ranges (Calvert 2001), but the direction of migrant *P. rapae* varied from west through north to east and they did not appear to utilize the physiographic features. The direction vectors for trans-Pyrenean spring migrant *P. rapae* tended to move away from the sun. This suggests the lack of a sun compass, such as that observed in *D. plexippus* (Perez et al. 1997). The fact that Pyrenean migration continues under partly cloudy conditions but stops under complete cloud cover, suggests that the butterflies may use polarized light, and that an alternate system such as a magnetic compass (Etheredge et al. 1999), which would function under cloud cover, is not available to them. The short migration by Pyrenean butterflies relative to that of *D. plexippus* may explain the lack of multiple guidance

systems, but the nature of the orientation-navigation system is unknown.

Migrating Pyrenean *P. rapae* require little energy for vertical movement. Based on the data of Marden (1987) and Ellington (1991), an adult *P. rapae* weighing 40 mg has 5×10^{-4} watts power during flight. Therefore, the work done to raise a butterfly 1000 m equals the power output during 13 minutes of flight. (This does not mean that the butterfly can ascend 1000 m in 13 minutes - it is a measure of the work done against gravity.) Therefore, assuming no wind, a butterfly which migrates 40 km across the central Pyrenees at a flight speed of 8 km/h devotes 5 hours' power to horizontal translation and perhaps 20 minutes' power to vertical ascent, and some of the work done against gravity can be recovered during subsequent descent. This explains why *P. rapae* can afford to fly over the Pyrenees rather than follow the valley bottom.

Pieris rapae in England and Australia are non-migratory, but the difference in the directional bias of individuals relative to migratory populations is a matter of degree. Baker (1978) observed that preferred directions of *P. rapae* in England are biased towards NNW in spring, and conversely in autumn. It is unclear whether the bias occurs on all days, or only on some. Similarly, Jones et al. (1980) observed a northward bias on some days at Canberra. In both cases, despite the bias, there were individuals with preferred directions all round the compass. Only a limited set of directions are followed during migration. However, the bias in the preferred direction of non-migrant populations suggests that non-migrant *P. rapae* are pre-adapted to migration.

Migration appears to require no new characteristics of movement, only an exaggerated degree of bias in individual directions; but the cues which determine the sex ratio of migrants, and the start, end, and direction of migration remain unknown. Furthermore, general problems of migration remain unresolved. Although the trans-Pyrenean migration is two-way, different individuals travel north and south, so the origin of the behavior is hard to explain in terms of individual selection. Similarly, it is difficult to explain the movement of *P. rapae* in Florida which is predominantly northwards in the spring, with little autumn return (Williams 1958, Walker 1991).

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LITERATURE CITED

- BAGUETTE, M., & G. NÈVE. 1994. Adult movements between populations in the specialist butterfly *Proclossiana eunomia* (Lepidoptera, Nymphalidae). *Ecol. Entomol.* 19:1-5.
- BAKER, R. R. 1978. *The Evolutionary Ecology of Animal Migration*. Hodder and Stoughton, London. 1012 pp.
- CALVERT, W. H. 2001. Monarch butterfly (*Danaus plexippus* L., Nymphalidae) fall migration: flight behavior and direction in relation to celestial and physiographic cues. *J. Lep. Soc.* 55:162-168.
- CRANK, J. 1975. *The Mathematics of Diffusion*. Clarendon, Oxford. 414 pp.
- CROMARTIE, W. J. 1975. Influence of habitat on colonization of collar plants by *Pieris rapae*. *Environ. Entomol.* 4:783-784.
- ELLINGTON, C. P. 1991. Limitations on animal flight performance. *J. Exp. Biol.* 160:71-91.
- ETHEREDGE, J. A., S. M. PEREZ, O. R. TAYLOR & R. JANDER. 1999. Monarch butterflies (*Danaus plexippus* L.) use a magnetic compass for navigation. *P. Nat. Acad. Sci. USA* 96:13845-13846.
- GILBERT, N. 1988. Control of fecundity in *Pieris rapae*. V. Comparisons between populations. *J. Anim. Ecol.* 57:395-410.
- GILBERT, N. & D. A. RAWORTH. 1996. Insects and temperature - a general theory. *Can. Entomol.* 128:1-13.
- GILBERT, N., A. P. GUTIERREZ, B. D. FRAZER & R. E. JONES. 1976. *Ecological Relationships*. W. H. Freeman and Co., Reading. 157 pp.
- GRAY, J. H., M. LOCKE & C. D. PUTNAM. 1953. Insect migration in the Pyrenees. *The Entomologist* 86:68-75.
- HADDAD, N. 2000. Corridor length and patch colonization by a butterfly, *Junonia coenia*. *Conserv. Biol.* 14:738-745.
- HERTZ, M. 1927. Bewegungen von Kohlweisslingen über einem Feld. *Biol. Zentralbl.* 47:569-570.
- HILL, J. K., C. D. THOMAS & O. T. LEWIS. 1996. Effects of habitat patch size and isolation on dispersal by *Hesperia comma* butterflies: implications for metapopulation structure. *J. Anim. Ecol.* 65:725-735.
- JONES, R. E. 1977. Movement patterns and egg distribution in cabbage butterflies. *J. Anim. Ecol.* 46:195-212.
- JONES, R. E. 1987. Behavioural evolution in the cabbage butterfly (*Pieris rapae*). *Oecologia* 72:69-76.
- JONES, R. E., N. GILBERT, M. GUPPY & V. NEALIS. 1980. Long-distance movement of *Pieris rapae*. *J. Anim. Ecol.* 49:629-642.
- JONES, R. E., J. R. HART & G. D. BULL. 1982. Temperature, size and egg production in the cabbage butterfly, *Pieris rapae* L. *Aust. J. Zool.* 30:223-232.
- LACK, D. & E. LACK. 1951. Migration of insects and birds through a Pyrenean pass. *J. Anim. Ecol.* 20:63-67.
- MARDEN, J. H. 1987. Maximum lift production during takeoff in flying animals. *J. Exp. Biol.* 130:235-258.
- MORAN, P. A. P. 1968. *An Introduction to Probability Theory*. Clarendon, Oxford. 542 pp.
- PEREZ, S. M., O. R. TAYLOR & R. JANDER. 1997. A sun compass in monarch butterflies. *Nature* 387:29.
- ROOT, R. B. & P. M. KAREIVA. 1984. The search for resources by cabbage butterflies (*Pieris rapae*). *Ecology* 65:147-165.
- SCHTICKZELLE, N. & M. BAGUETTE. 2003. Behavioural responses to habitat patch boundaries restrict dispersal and generate emigration-patch area relationships in fragmented landscapes. *J. Anim. Ecol.* 72:533-545.
- SNOW, D. W. & K. F. A. ROSS. 1952. Insect migration in the Pyrenees. *Entomol. Mon. Mag.* 88:1-6.
- SPIETH, H. R. & A. KASCHUBA-HOLTGRAVE. 1996. A new experimental approach to investigate migration in *Pieris brassicae* L. *Ecol. Entomol.* 21:289-294.
- SUTCLIFFE, O. L. & C. D. THOMAS. 1996. Open corridors appear to facilitate dispersal by ringlet butterflies (*Aphantopus hyperantus*) between woodland clearings. *Conserv. Biol.* 10:1359-1365.
- WALKER, T. J. 1991. Butterfly migration from and to peninsular Florida. *Ecol. Entomol.* 16:241-252.
- WILLIAMS, C. B. 1958. *Insect Migration*. Collins, London. 235 pp.
- WILLIAMS, C. B., I. F. B. COMMON, R. A. FRENCH, M. MUSPRATT & M. C. WILLIAMS. 1956. Observations on the migration of insects in the Pyrenees in the autumn of 1953. *T. Roy. Ent. Soc. London.* 108:385-407.

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